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Research Article

Similar drivers but distinct patterns of woody and herbaceous alien plant invasion

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Abstract

The extent of alien plant invasion and numbers of invasive species are increasing, exacerbating invasion impacts. Effective and efficient management requires understanding the drivers and distribution of plant invasions at the landscape scale. In this study, we used a species distribution modelling approach to determine whether the patterns and correlates of alien invasion vary by plant growth form. Focusing on the occupancy and proportional cover of forbs, graminoids and woody vegetation, we used boosted regression trees (BRTs) to characterise alien plant invasion risk in two major catchment regions in Victoria, Australia. Of 7,630 quadrats surveyed between 1970 and 2019, 69% contained alien plants, with forbs being the most prevalent growth form. Alien plants constituted 22% of the total number of plant species recorded. Alien species cover varied widely, with alien species contributing between 0.2% to 100% of vegetation cover in a plot. Alien forbs and graminoids had higher mean cover compared to alien woody plants. Abiotic conditions, particularly temperature and precipitation, had the greatest influence on alien plant invasion overall, explaining 41–76% of observed variation. Summer mean maximum temperature was a strong predictor across all growth forms. Areas with higher vegetation cover (native + alien species) were predicted to have higher occupancy, but lower proportional cover, of alien forbs and graminoids. In contrast, alien woody plants had a negative relationship with woody vegetation cover. High levels of invasion were predicted in areas with intensive land use, such as urban and agricultural zones. Forbs had a high probability of occupancy throughout the region, even in higher elevations, while graminoids and woody vegetation were more restricted to lower elevations and areas characterized by human activity. The study highlights that alien plant invasion is influenced by a complex interplay of abiotic factors, propagule pressure, human activity and biotic conditions. The findings underscore that, while there are common drivers across growth forms, specific patterns and influences vary. For instance, alien forbs were more widespread but less dominant in areas with high vegetation cover, while alien woody plants were less common and more constrained by vegetation than the other two growth forms. Management strategies should prioritise maintaining and restoring native vegetation to limit the dominance of alien species and controlling invasive plants after disturbance. Although single-species models remain valuable, our study shows that species distribution models based on growth form offer a practical approach for assessing plant invasions across diverse landscapes.

Key words: Alien vegetation management, Boosted Regression Trees, ecosystem invasibility, habitat suitability models, invasive plant species risk, plant growth form, species distribution models

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Introduction

Increases in trade and travel have increased incidence of human-mediated alien species introduction and human-induced environmental change has facilitated higher rates of alien plant establishment (Seebens et al. 2018; Pyšek et al. 2020b). Invasive alien species, including plants, are considered one of the major threats to global biodiversity and have the potential to cause substantial environmental and economic damage (Diagne et al. 2021; Novoa et al. 2021; IPBES 2023). In Australia alone, estimates of the cost of alien plant invasions exceed AU$13.6 billion per year (Hoffmann and Broadhurst 2016), with totals of at least AU$299 billion since the 1960s (Bradshaw et al. 2021). The efficient and effective management of alien species is of high economic, social and ecological importance. However, to manage alien plant species effectively, it is vital to understand what drives invasion, how these drivers might differ across different groups of plants and how this information can be used to spatially predict the occupancy and abundance of alien plants.

Many ecosystems are invaded by multiple alien plant species (Kuebbing et al. 2013) and vegetation management organisations are often mandated to control multiple invasive species across a landscape (Brandt et al. 2023). Invasive species management is more cost effective when multiple species are managed in concert, rather than individually (Januchowski-Hartley et al. 2011; Lohr et al. 2017). Effective spatial prioritisation of invasive species control requires information about where alien plants occur in the landscape, enabling hotspots of invasion to be targeted. Given the limited availability of vegetation surveys and the imperfect data on invasive species distributions, there is a need for predictive models that can estimate areas likely to experience high levels of invasion. Such approaches must be applicable to a wide range of plant species and habitats. However, understanding about the factors that drive alien plant invasions across various landscapes remains limited and even less is known about how these drivers may differ across plant growth forms.

Species distribution models (SDMs) are commonly used to predict the spatial distribution of individual invasive species (Ficetola et al. 2007; Srivastava et al. 2019). However, SDMs can be data- and resource-demanding and, when built for individual species, many SDMs would be required to provide a general picture of alien plant invasion. For example, based on the number of recorded alien graminoid species, at least 175 individual SDMs would be required to estimate the spatial distribution of alien graminoids that occur in a 42,000 km^2 region of Victoria, Australia. Increasing the number of SDMs can increase the amount of time spent preparing the models and interpreting and integrating their results, and the lack of temporally and spatially unbiased data for individual species could result in unreliable predictions (Cordier et al. 2020). Trait-based studies that examine characteristics associated with species invasiveness provide insight into general drivers of plant invasion, combining data from tens to hundreds of species (Catford et al. 2016; Fristoe et al. 2021; Palma et al. 2022). However, these studies also demand considerable amounts of data and most trait-based studies do not provide spatially-explicit predictions (Catford et al. 2019; Junaedi et al. 2021; Palma et al. 2021).

A major axis of variation amongst plants is growth form, with different growth forms responding to environmental gradients and anthropogenic pressures in distinct ways (Giorgis et al. 2016; Šímová et al. 2018; Bartlett et al. 2023). In invasion ecology, classifying alien plant species by growth forms – such as forbs,

graminoids and woody plants – can facilitate understanding of their responses to socioecological factors. Species within the same growth form often have similar functional traits or invasions histories (e.g. pathways of introduction; Bartlett et al. (2023)) that influence their invasiveness and interactions with the environment (Giorgis et al. 2016; Šímová et al. 2018). Therefore, grouping alien plant species by growth forms can be a useful approach for predicting their relationships with environmental variables, as it can account for shared functional traits that influence invasion success.

Growth form information is readily available for all known taxa (e.g. trees, shrubs, forbs, graminoids). When combined with species occupancy and abundance records, this enables group-based distribution models of invasion risk on a landscape scale (Catford et al. 2011). Growth form-based distribution models could enable spatial prioritisation of multi-species alien vegetation management without the need to build hundreds of individual SDMs and could provide results that are widely understood by researchers, practitioners and the general public. By considering these growth forms, researchers can better predict and manage the spatial patterns of alien plant invasions, as each group may respond differently to environmental predictors such as climate, soil type and disturbance regimes. Functional grouping can thus enhance the accuracy and applicability of predictive models across diverse landscapes and plant species.

In this study, we use a species distribution modelling approach to determine whether the patterns and correlates of alien invasion vary by plant growth form. Focusing on the occupancy and proportional cover abundance of forbs, graminoids and woody vegetation, we use boosted regression trees (BRTs) to characterise alien plant invasion risk in two major catchment regions in Victoria, Australia to address two questions:

1) How does the relative influence of variables linked to propagule pressure, human disturbance, biotic and abiotic characteristics differ amongst alien forbs, graminoids and woody vegetation?
2) How do spatial patterns in alien plant invasion differ amongst the three growth forms?

We focus on the proportion of vegetation cover that is made up of alien plants as this indicates relative dominance (Catford et al. 2012; Seabloom et al. 2013, 2015). To provide context, we also examine the observed level of invasion in the study region (including alien species richness, % of surveyed plots that were occupied by alien plants, proportion of vegetation cover made up of alien plants). Identifying how landscape vulnerability to invasion varies between different plant growth forms will enable more efficient mapping and monitoring techniques, facilitating management prioritisation (Foxcroft et al. 2017)

Materials and methods

Study region

This study focuses on a region encompassing two Catchment Management Authorities within Victoria, south-eastern Australia: West Gippsland and Goulburn Broken (Fig. 1). The Catchment Management Authorities are responsible for

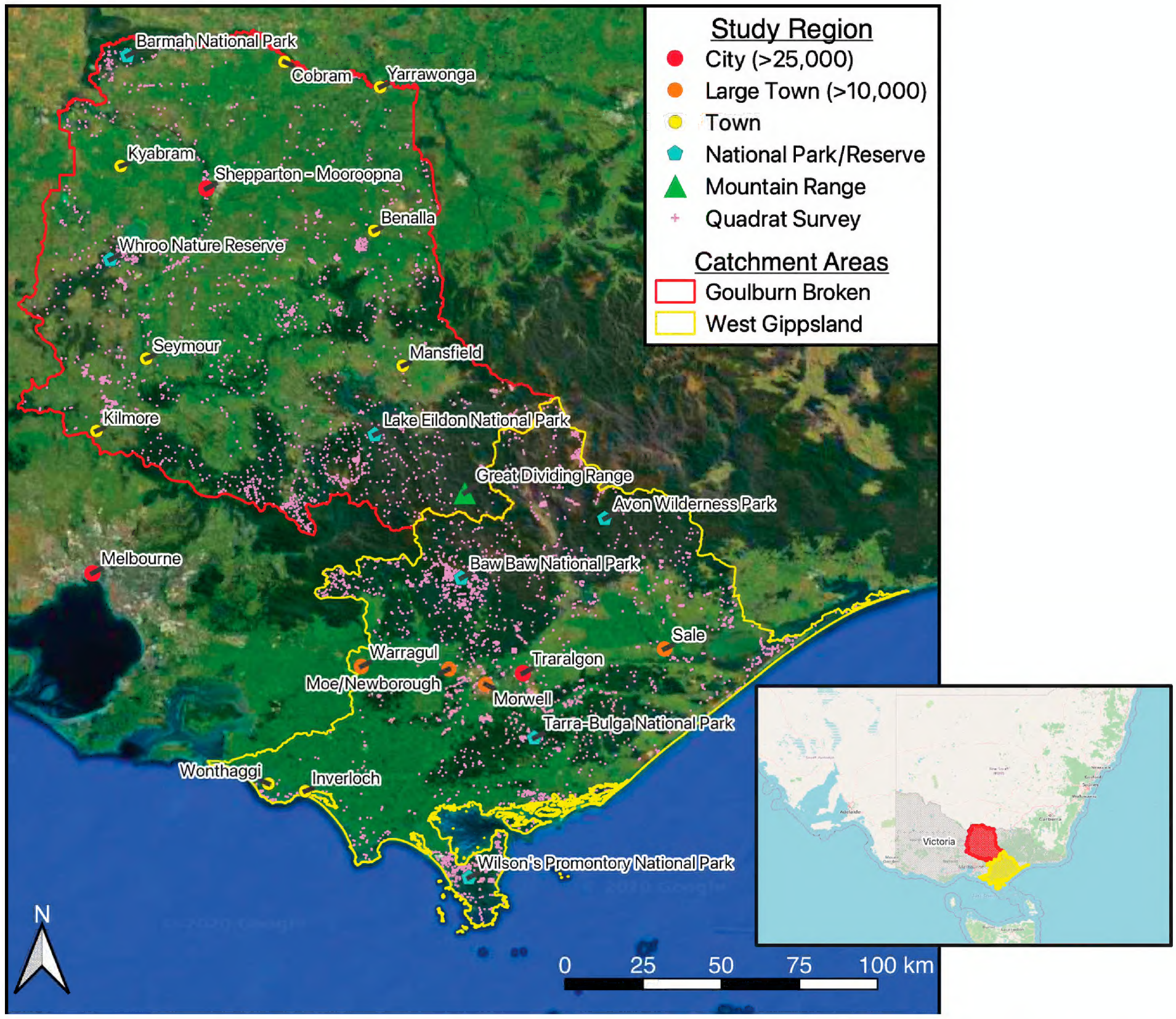

Figure 1. A map of the study region in Victoria, south-east Australia. The map illustrates areas of the two Catchment Management Authorities: Goulburn Broken (outlined in red) and West Gippsland (outlined in yellow), which were combined to create the study region. The map highlights the main characteristics of the study region including major towns and cities, roads, national parks, landforms and locations of the 7,630 vegetation quadrat survey sites.

planning and coordination of environmental management within their catchments. West Gippsland (~ 17,700 km^2) stretches from the Bass Strait coast in the south to the Great Dividing Range where it borders with Goulburn Broken (~ 24,300 km^2), which extends to the agricultural floodplains of the River Murray in the north. The study area covers a latitude range of approximately -39.16 to -35.8 and a longitude range of 144.7 to 148.0.

The southern catchment management area in the study region (West Gippsland) experiences dry hot summers with the majority of the ~ 850 mm annual rain occurring in winter months, with the central uplands often receiving triple that of the southern lowlands (Bureau of Meteorology and CSIRO 2019b).The historical mean daily minimum July temperature for Morwell, a central West Gippsland town, is 3.7°C, while the historical mean daily maximum January temperature is 26.7°C. The climate of the northern catchment area (Goulburn Broken) varies with topography resulting in annual rainfall ranging from 1600 mm at Lake Mountain to 460 mm in Kyabram in the

north (Bureau of Meteorology and CSIRO 2019a). The historical mean daily minimum July temperature for Shepparton, a central Goulburn Broken town, is 3.4°C, while the historical mean daily maximum January temperature is 32.0°C (Bureau of Meteorology 2025).

Geology across the study region varies from clay, to granite, siltstone, mudstone, silt, sand and sandstone (Geoscience Australia 2021). The study region has a total population of approximately 415,000 people who mainly reside in regional cities and rural towns (WGCMA 2019). More than 50% of land is under private ownership and is mainly used for agriculture resulting in habitat fragmentation. Public lands associated with the Great Dividing Range experience significantly lower levels of human activity (GBCMA 2013; WGCMA 2019).

The study region contains a variety of habitats ranging from coastal salt marshes, mangroves and heathlands in the south to alpine and heavily forested regions in the centre to floodplain forests and semi-arid woodlands in the north. The study region was selected based on its wide variety of environmental and anthropogenic conditions, high levels of invasion and invasive plant management interest from management agencies.

Response variables

We used vegetation survey data from 7,630 quadrats between 1970 and 2019 by the Victorian Department of Energy, Environment and Climate Action (DEECA). These data provide information on plant species occupancy (presence/absence) and species cover abundance for all native and alien (non-native to Australia) plant species in the study region.

The coordinates of the centre of each 30 m × 30 m quadrat were recorded with either a map (pre-1993: ± 100 m accuracy) or Geographical Positioning System (post 1993 ± 7 m accuracy). Foliage cover of all plant taxa found within the quadrats was estimated using the Braun-Blanquet scale (Kent and Coker 1992). For statistical analysis, Braun-Blanquet scale values were converted to percentages on a proximal ordinal scale (+: 1%, 1: 2%, 2: 10%, 3: 30%, 4: 60%, 5: 80%) to estimate growth form and total vegetation cover abundance for each quadrat. Total cover abundance values per quadrat could exceed 100% where multiple layers of vegetation (e.g. ground and aerial cover) were present.

The cover abundance of combined alien taxa was then calculated as a percentage of total (i.e. native and alien) plant cover. Alien forb, graminoid (Poaceae, Juncaceae, Cyperceae) and woody (trees, shrubs) plant cover was expressed as a percentage of the total cover for their respective growth form. We classified alien plant species according to their dominant growth form (i.e. forbs, graminoids or woody), a widely used functional categorisation that captures key ecological and phylogenetic differences amongst species (Giorgis et al. 2016; Šímová et al. 2018; Bartlett et al. 2023). Growth form is a tractable and widely available trait, offering high data coverage across large species pools, and is frequently used in invasion ecology to provide generality beyond species-specific studies. Moreover, growth forms are readily understood by practitioners and land managers, enabling direct application of findings to policy and management contexts. While studies using continuous traits can offer fine-scale resolution, they are often limited by data availability and complexity (Palma et al. 2021, 2022). Our growth-form-based approach thus balances ecological interpretability, methodological accessibility and relevance to applied conservation.

By producing alien cover abundance as a proportion of total cover, alien species contribution to the surrounding flora community can be better understood (Catford et al. 2011, 2012). As has been discussed and demonstrated in previous studies (e.g. Catford et al. (2012); Seabloom et al. (2013); Seabloom et al. (2015)), proportional alien cover can effectively indicate relative dominance of vegetation by exotic species. Although exotic species richness can be correlated with exotic species abundance, that is not always the case (Seabloom et al. 2013; Seabloom et al. 2015); for example, one invasive alien species could potentially contribute more cover than 10 non-invasive alien species. We thus focus on alien cover rather than alien species richness.

Environmental variables

We assembled a range of environmental variables as proxies for propagule pressure, human activity, abiotic and biotic conditions that are likely to influence alien plant invasion (Catford et al. 2009; Catford et al. 2011; Szymura et al. 2018; Pyšek et al. 2020a). Raw data for over 30 variables was sourced from governmental datasets (i.e. from DEECA and the opensource https://www.data.vic.gov.au/database) before being compiled in QGIS 3.14 where variable data were sampled for each quadrat survey location. Although boosted regression trees (BRTs) are robust to effects of moderate multicollinearity amongst independent variables (Elith et al. 2008), we used correlation analysis and the literature to reduce the number of variables to avoid model overfitting (De Marco and Nóbrega 2018). Correlation analysis highlighted variables with high levels of correlation (Pearson correlation coefficient > |0.7|). When multicollinearity was found, the more distal variable(s) were removed in favour of the more proximal one(s). For this reason, temperature and rainfall variables were chosen ahead of latitude and longitude due to their more proximal influence on plant growth. The model for combined alien taxa included 19 variables and the models for woody, forb and graminoids included 20 environmental variables following the addition of a variable for each specific growth form (Table 1). For individual growth form models, we included the additional specific growth form variable to understand the influence on growth form-specific habitat suitability and competition on the alien growth form occupancy and cover levels.

The land-cover classifications used in this study were split into five-year periods between 1985–2019 and contained 19 land-cover categories (Table 1; Suppl. material 1: table S1). By selecting the land-cover period closest to that of the survey date, land-cover classification accuracy at each quadrat site was maximised. To ensure the invasion models can be predicted over large regions, not just small specific areas, the land-cover categories used were broad enough to be used internationally across various climatic environments (e.g. "urban", "irrigated horticulture", "native trees"; see Suppl. material 1: table S1).

Gap analysis

We undertook gap analysis to ensure the training data on which the model was built (i.e. quadrat survey locations) encompassed the full extent of environmental conditions present across the study region. We compared the maximum, minimum and mean values of environmental variables in the quadrat survey data to those of the broader study region to ensure representativeness. The environmental conditions

Table 1. Independent variables used in the study and their corresponding number ID and descriptive statistics. Factor: B indicates biotic conditions; A indicates abiotic conditions; P indicates propagule pressure; H indicates human activity. Because vegetation layers can overlap, vegetation cover can exceed 100%. Longer descriptions of the independent variables can be found in Suppl. material 1: table S1 and their correlations in Suppl. material 1: fig S1.

ID	Independent Variable	Brief Description	Factor	Mean (SE)	Range
1	Absolute forb cover	Total forb overlapping cover in quadrat (native + alien species)	B	25.7% (0.3)	1–290%
2	Absolute graminoid cover	Total graminoid overlapping cover in quadrat (native + alien species)	B	32.2% (0.4)	1–317%
3	Absolute woody vegetation cover	Total woody overlapping cover in quadrat (native + alien species)	B	57.7% (0.5)	1–425%
4	January mean maximum temperature	Mean maximum temperature in January	A	24.2°C (0.04)	15.7–30.9°C
5	Land-use intensity	Parcel size is a commonly used proxy for land-use intensity. Area (ha) of each parcel in Victoria, Australia	P, H	2332.0 ha (47)	0.643–26526.5 ha
6	Survey year	Year in which 30 m × 30 m quadrat survey was undertaken	P	1996 (0.1)	1972–2019
7	Geology	The surface geology of the study area	A	Sandstone (Mode)	See Suppl. material 1: table S1
8	Land cover	Land-cover categories that most closely correspond to survey year	P, A, H	Native Trees (Mode)	See Suppl. material 1: table S1
9	Absolute vegetation cover	Total vegetation overlapping cover in quadrat (native + alien species)	B	120% (0.6)	1–665%
10	Wind exposition	Wind effect index. Reflects a locations general exposure to wind. Unitless	P, A	1.1 (0.002)	0.8–1.4
11	January mean rainfall	The mean rainfall in January	A	58.3 mm (0.2)	28–103 mm
12	Radio-element Thorium	Radiometric data: Gamma radiation of Thorium (proxy for soil texture, Read et al. (2018))	A	8.6 ppm (0.06)	-0.26–38.7 ppm
13	= Height Above River (HAR)	Log Vertical height above river in metres. Unitless	A	0.79 (0.002)	0–1.0
14	Normalised Difference Vegetation Index (NDVI)	The median Normalised Difference Vegetation Index. Unitless	B	0.67 (0.002)	-0.33–0.91
15	Road-demographic cost distance analysis	Summation of 5 cost-distance variables. Unitless	P, H	11.2 (0.02)	0–15.1
16	July mean rainfall	The mean rainfall in July	A	101 mm (0.6)	38–223 mm
17	Distance to river	Distance to nearest watercourse	P, A	0.43 km (0.01)	0–11.2 km
18	Time since fire	Time since last wildfire	A	35 years (0.4)	0–98 years
19	Diurnal anisotropic heating x ruggedness index	Diurnal Anisotropic Heating multiplied by a Ruggedness Index. Unitless	A	0.01 (0.0001)	0.3×10^{-5}–0.09
20	July mean minimum temperature	Mean minimum temperature in July	A	2.9°C (0.02)	-2.7–6.7°C
21	Historical land use 1888	Land use in 1888 (Sinclair et al. 2012)	P, A, H	Dryland Agriculture (Mode)	See Suppl. material 1: table S1
22	Topographic wetness index	Soil moisture index. Unitless	A	0.62 (0.002)	0.18–1.0

observed in the quadrats represented up to 100% of the environmental variation in the study region. No variables exceeded 100%, confirming that the models did not extrapolate beyond the conditions found in the training data.

Modelling

We ran eight models, using boosted regression trees (BRTs), to model relationships between the environmental variables and the occupancy and cover abundance of combined alien taxa, and alien forbs, graminoids and woody vegetation growth forms. BRTs use a two-stage modelling method, which fits a series of simple regression tree

analyses and then combines their results in a forward stage-wise manner using iterative machine-learning algorithms to maximise predictive power with high accuracy (De'ath 2007). BRTs are robust when modelling ecological data due to their ability to handle various data types (continuous and discrete), missing data and non-linear relationships, whilst providing strong performing predictive and explanatory models (Elith et al. 2008). BRTs also allow for easy graphical and numerical interpretation of complex relationships between independent variables, making them particularly suitable for studying alien invasion (De'ath 2007; Elith et al. 2008).

This study followed the BRTs methods set out by Elith et al. (2008) and Elith and Leathwick (2017) to model the relationships between independent variables and alien plant invasion. BRTs for alien occupancy and cover abundance were run separately, with the cover abundance models only using quadrats where alien species were present. The separation of occupancy and cover abundance models overcomes issues associated with data containing a high zero count, allows easy interpretation and also provides insight into how invasion drivers differ amongst invasion metrics (Catford et al. 2012). Occupancy models provide insight into alien species ability to occupy sites and thus tolerate their biotic and abiotic conditions, while cover abundance models indicate when an alien species becomes dominant at a site, resulting in increased impacts on the native ecosystem structure and function.

BRTs were run in R (version 1.3.1056) using packages "gbm" (version 2.1.8; Ridgeway (2019)) and "dismo" (version 1.1–4; Hijmans et al. (2017)) and code provided in Elith et al. (2008) and Elith and Leathwick (2017). Bernoulli (binomial) and Gaussian error distribution models were fitted for occupancy and cover abundance models respectively. To improve model performance, cover abundance models for combined alien taxa and alien growth forms (forbs, graminoids and woody vegetation) were log-transformed to normalise residuals. BRT models were adjusted to maximise performance with alien plant occupancy models run using a learning rate of 0.01, a tree complexity of four and a bag fraction of 0.7 to maximise predictive performance, following Catford et al. (2011). The parameters remained the same for the alien proportional cover models except for tree complexity, which was increased to five.

We conducted a Moran's I test (Moran 1950), using the "spdep" package in R (Bivand et al. 2013), to examine for spatial autocorrelation in the models (see Suppl. material 1: appendix S1). To ensure that there were no zero-neighbour locations or disconnected subgraphs across all models, the nearest-neighbour distance was set to 0.2 degrees (~ 22 km). Although statistically significant in several occupancy models, the magnitude of Moran's I was consistently low (all < 0.04), indicating that, while spatial structure exists, it is unlikely to meaningfully bias predictions or invalidate model assumptions (Legendre and Fortin 1989; Dormann et al. 2007). No corrective spatial modelling (e.g. spatial eigenvector filtering, spatially-explicit models) was therefore necessary, though we note that there was some weak spatial structure in the occupancy models.

To assess whether the use of a 49-year dataset (1975–2023) introduced temporal biases, we re-ran all BRT models using a temporally restricted dataset covering 1988–2003. This 16-year subset captures the period with the highest survey density and represents a broad range of environmental variation. The results from the temporally restricted dataset were then compared to the main model outputs (see Suppl. material 1: fig S2). This comparison confirmed that sampling bias was not responsible for driving the relationships between environmental predictors and alien plant occupancy and relative cover.

Model evaluation

We used two performance metrics to select the best performing models for each dependent variable:

1. Percentage deviance explained, expressed as a percentage of the null deviance for each response variable (Leathwick et al. 2008), provided a 'goodness-of-fit' metric by predicting to data excluded from the original model training data.
2. Area Under the receiver operating Characteristic curve (AUC) was used to determine occupancy models' ability to discriminate between quadrats with or without alien species. AUC is generated during the random cross-validation analysis. An AUC score of 1.0 indicates perfect discrimination and a score of 0.5 suggests no discrimination accuracy (Leathwick et al. 2008).

We also undertook random Cross-validation (CV) correlation analysis to measure the correlation between predicted values and raw data not used in model training. CV is undertaken by randomly splitting the data into 10-folds and training the model on nine folds, with the final fold being used for testing. This testing was repeated a total of five times with the averages being used to display model performance.

Spatial predictions

We then used these models to predict occupancy and cover abundance of three plant growth forms (forbs, graminoids and woody vegetation) across the study region in Victoria, Australia. The predictions were mapped using the "raster" package in R (version 3.3–13; Hijmans (2019)), providing spatial predictions of the combined alien taxa and individual growth forms' probability of occupancy and expected proportional cover. Spatial resolution was limited to 50 m × 50 m due to the resolution of the independent variables. All independent variables were processed into raster layers clipped to the extent of the study region. For independent variables where there is not total coverage (e.g. total vegetation cover and growth form vegetation cover), no data values were included to ensure no data values were not interpreted as zeros. Expected cover was produced by multiplying the predicted percentage cover by the probability of an alien species being present, following the approach of Catford et al. (2011).

Results

Level of invasion

Of the 7,630 quadrats surveyed, 69% contained alien plant species and alien species made up 22% of the 3,087 plant species recorded (688 alien species, of which 14.2% were woody plants, 25.4% graminoids and 71.7% forbs). The mean species richness across all quadrats was 28.4 (0.16 SE), ranging from 1–115 species. Total vegetation cover was weakly correlated with species richness ($r = 0.248$; $P < 0.001$), but no relationship was found with total vegetation cover and alien species richness ($r = 0.067$; $P < 0.001$). When examining only the 5,239 quadrats that contained alien species, the mean alien proportional cover was 16.67% (0.31% SE), but this ranged from 0.19–100%, while the mean alien species richness per quadrat was 6.6 (0.09 SE) and ranged from 1–45 species.

Total vegetation cover was strongly correlated with total native cover (r = 0.877; $P < 0.001$), but had a weaker correlation with total alien cover (r = 0.263; $P < 0.001$) and alien proportional cover (r = -0.078; $P < 0.001$). Both alien proportional cover and alien proportional species richness were negatively correlated with total native cover and native species richness.

Relative influence of environmental variables on level of invasion

The BRT models performed well, with models fit in the CV analyses accounting for 38.0–59.4% of the reduction in the null deviance, with CV correlations of between 0.62 and 0.78 and AUC scores of between 0.90 and 0.94. As expected, all eight BRT models demonstrated that alien plant occupancy and cover were linked to numerous biotic and abiotic factors, propagule pressure and human activity (Fig. 2). Although the relative influence of specific variables varied somewhat across response variables (most notably in relation to vegetation cover, as discussed below), drivers of forb, graminoid and woody invasion were similar overall (Fig. 2). Variables representing abiotic conditions had the strongest influence on invasion overall, with their summed relative influences ranging from ~ 41% to ~ 76% (Fig. 2). The alien forb occupancy model differed, however, having the strongest association with biotic conditions (B) with summed relative influences of 47.7% (see Suppl. material 1: table S2).

January (summer) mean maximum temperature was amongst the top two most influential variables in six of the eight models and amongst the top six variables in the remaining two models. Relationships between January mean maximum temperature and invasion were very similar across all response variables; occupancy and cover of combined alien taxa and individual growth forms increases sharply at ~ 23°C January mean maximum until levels plateaued around 25–26°C (Fig. 3).

For each alien growth form occupancy and cover model, total cover of the same growth form (e.g. summed absolute cover of alien and native forbs was used as an explanatory variable in models of alien forb occupancy and proportional cover) was amongst the top two most influential independent variables and the most influential biotic variable (Fig. 2), except for the woody vegetation occupancy model. The occupancy of combined alien taxa was positively associated with total vegetation cover, while proportional cover was negatively associated with total vegetation cover (Fig. 4). This trend extended to the relationships between alien forb and graminoid occupancy and proportional cover with their respective total growth form cover. As their respective growth form cover increased, the alien forb and graminoid occupancy increased, while their proportional cover decreased (Fig. 4). Unlike forbs and graminoids, both the occupancy and proportional cover of alien woody plants were negatively associated with total woody plant cover.

Survey year had a strong relationship with all alien cover variables, with cover increasing over time. The probability of alien occupancy rose gradually between 1972 and ca. 2015, after which it dropped sharply (Fig. 5).

Temporal consistency of invasion drivers

To ensure that relationships between alien plant growth forms and the environmental independent variables were not simply artefacts of spatial or temporal biases in the data collection, we re-ran all BRT models using a restricted dataset

spanning 1988–2003 – the period that captured most variation in environmental factors. These models yielded similar rankings of key predictors and comparable response patterns to those derived from the full 49-year dataset. While minor differences are expected due to the stochastic nature of BRT modelling, the overall ecological interpretations remained consistent (see Suppl. material 1: fig S2).

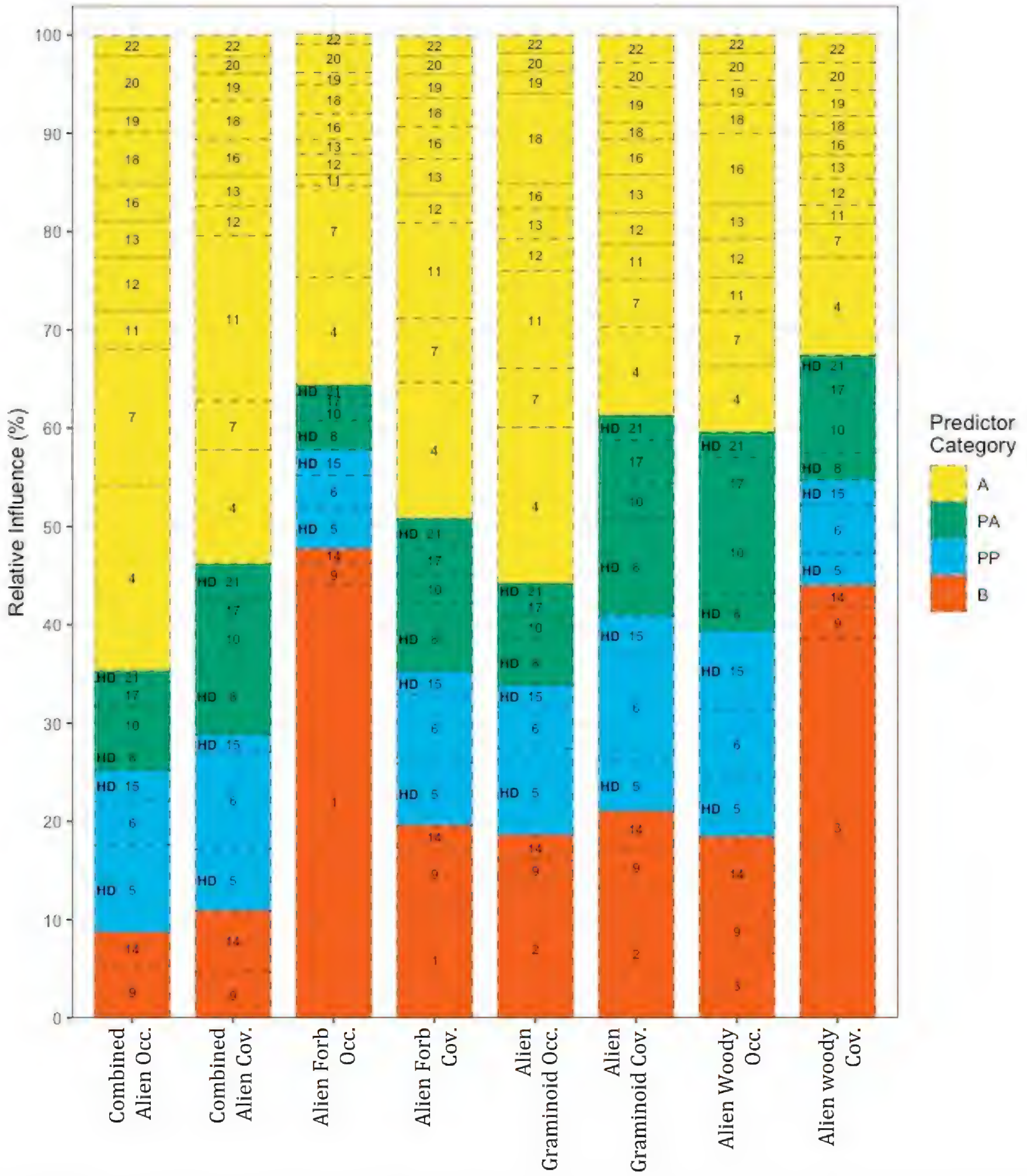

Figure 2. Stacked bar charts showing the relative explanatory power of the independent variables used to model the occupancy and cover of combined alien taxa, alien forbs, alien graminoids and alien woody vegetation across the study region. Variables were grouped by whether they represent: abiotic characteristics (A), propagule pressure and abiotic characteristics (PA), propagule pressure (PP), biotic characteristics (B). 'HD' indicates variables capturing human activity. Bracketed numbers relate to the independent variable numbers in Table 1. Models fit in the CV analyses explained 38.0–59.4% of the reduction in the null deviance, had CV correlations of between 0.62 and 0.78 and AUC scores of between 0.90 and 0.94. The difference between training AUC and CV AUC was always less than 0.01 suggesting overfitting of the models was not an issue.

Spatial predictions of invasion

Predictions of invasion indicate that, for almost any given location across the study region, there was a high probability of occupancy of alien species from at least one growth form, especially forbs (Fig. 6). Areas with higher elevation, sandplains and regions of low human settlement were predicted to have lower levels of alien plant occupancy and cover, although this pattern varied amongst growth forms. Alien graminoids and woody vegetation predictions indicated very low levels of invasion across the Great Dividing Range, but alien forbs still exhibited high occupancy in these higher elevation areas (Fig. 6c), though levels of alien forb cover remained

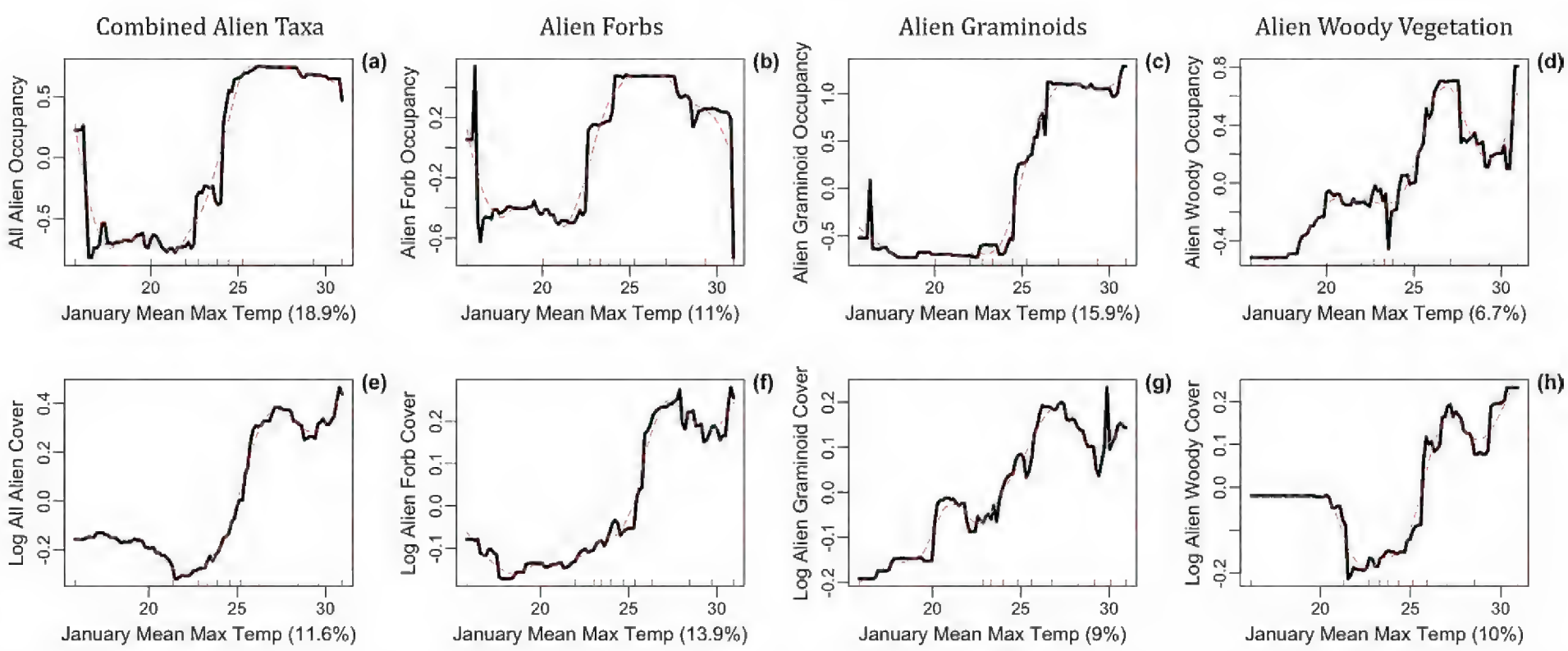

Figure 3. Partial dependence plots illustrating the marginal effect of mean maximum temperature in January on the probability of: **a.** Alien occupancy; **b.** Alien forb occupancy; **c.** Alien graminoid occupancy; **d.** Alien woody occupancy and the expected; **e.** Alien cover; **f.** Alien forb cover; **g.** Alien graminoid cover and **h.** Alien woody cover across the study region. Markings on the inner x-axis denote the training data deciles. Percentages represent the relative influence of mean maximum temperature in January on each model.

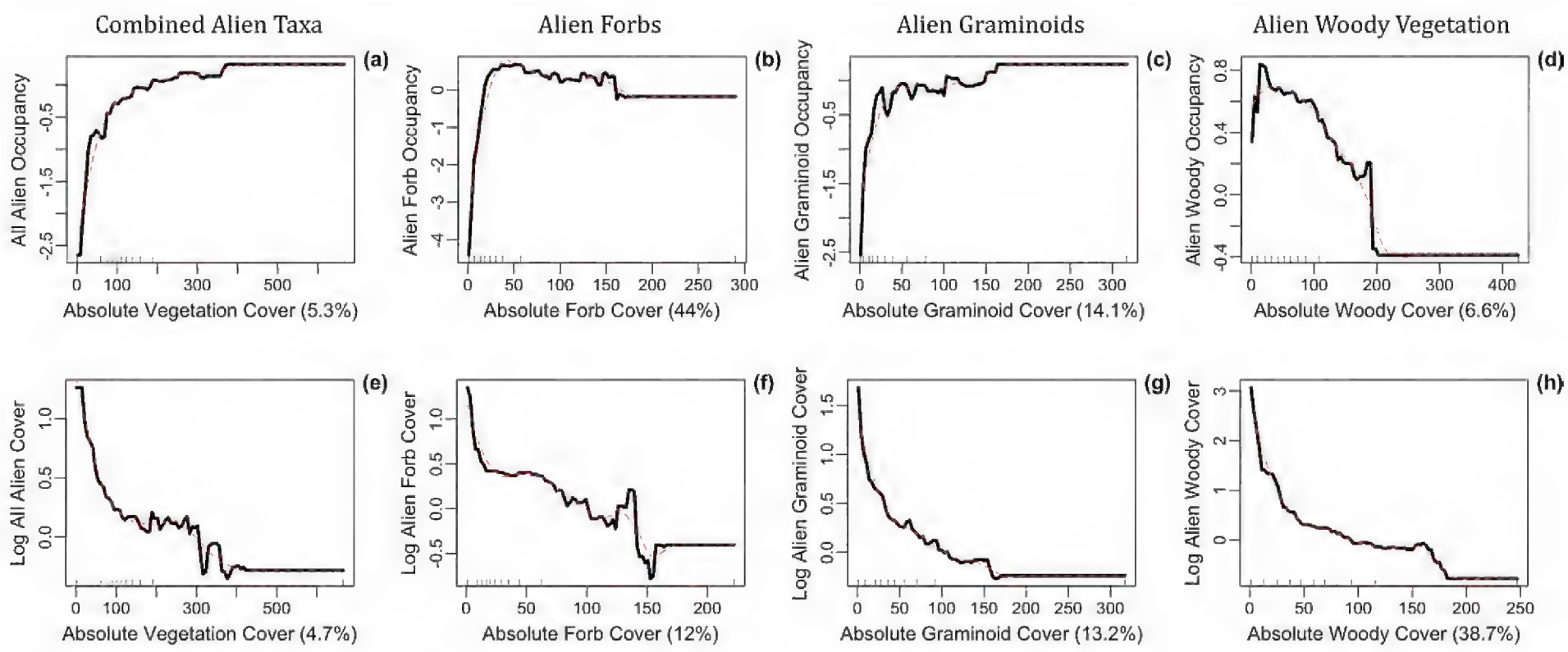

Figure 4. Partial dependence plots illustrating the marginal effect of total vegetation cover on: **a.** The probability of alien occupancy; **e.** Log-transformed alien cover; and the marginal effect of total growth form cover on the probability of: **b.** Alien forb occupancy; **c.** Alien graminoid occupancy; **d.** Alien woody occupancy and the expected; **f.** Log-transformed alien forb cover; **g.** Log-transformed alien graminoid cover and **h.** Log-transformed alien woody cover across the study region. Markings on the inner x-axis denote the training data deciles. Percentages represent the relative influence of absolute (growth form) vegetation cover on each model.

low (Fig. 6d). Despite the lower probability of alien taxa occupancy in the Great Dividing Range (> 500 m above sea level), probabilities still reached ~ 0.80 in areas of high vegetation cover (Fig. 6). This contrasts with combined alien cover, which remained very low (< 3.0% expected alien cover) across this elevated region and across national parks and reserves located in southern West Gippsland, which are characterised by high tree and vegetation cover (Figs 1, 6).

Consistent with the similarity in their drivers (Figs 2–5), predicted invasion levels were highly correlated across the eight response variables examined. Maps of combined alien taxa, alien forb and alien graminoid models displayed similar patterns of both occupancy and expected relative cover. Predicted invasion of alien woody vegetation was notably lower across the study region compared to forbs and graminoids (Fig. 6). Areas characterised by high levels of human activity and land-use intensity were predicted to have high levels of alien occupancy and cover. High land-use intensity areas, such as agriculture and urban areas, had the highest levels of predicted occupancy and cover (> 0.90 occupancy probability, > 50% cover), most notably for alien forb and graminoids where towns and cities (e.g. Mansfield, Seymour and Benalla in Goulburn Broken; Sale and Traralgon in West Gippsland) had predicted occupancy of > 0.90 and proportional cover levels were frequently > 70%. Despite woody vegetation invasion levels not being as high at these locations, urban regions were still more vulnerable to alien woody plant invasion (~ 0.70 occupancy probability; ~ 8% proportional cover) compared to more rural areas (< 0.45 occupancy probability; < 5% proportional cover).

Discussion

By examining drivers and patterns of plant invasion in south-eastern Australia, in this study we identified common themes in alien forb, graminoid and woody vegetation occupancy and abundance at the landscape-scale. While there was some variation in the influence of specific drivers across the eight response variables,

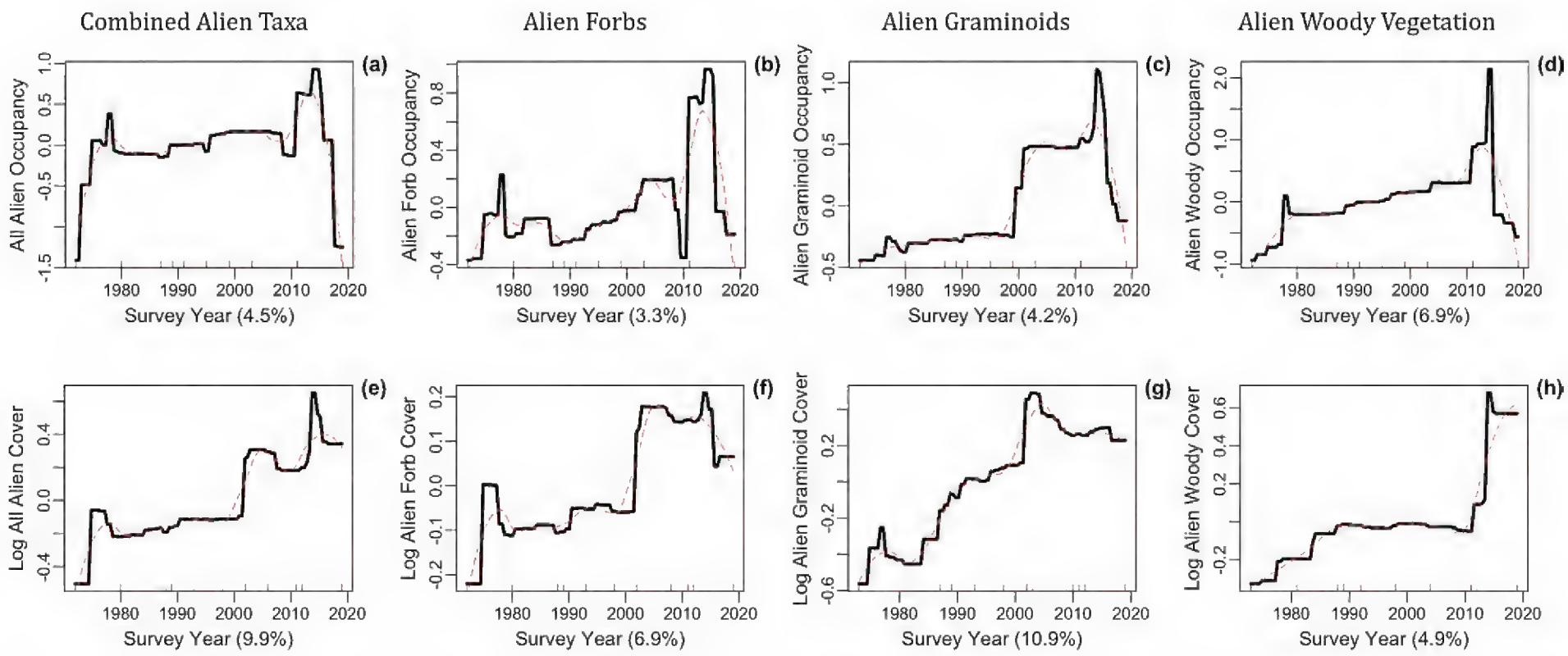

Figure 5. Partial dependence plots illustrating the marginal effect of survey year on the probability of: **a.** Alien occupancy; **b.** Alien forb occupancy; **c.** Alien graminoid occupancy; **d.** Alien woody occupancy and the log-transformed expected; **e.** Alien cover; **f.** Alien forb cover; **g.** Alien graminoid cover and **h.** Alien woody cover across the study region. Markings on the inner x-axis denote the training data deciles. Percentages represent the relative influence of survey year on each model.

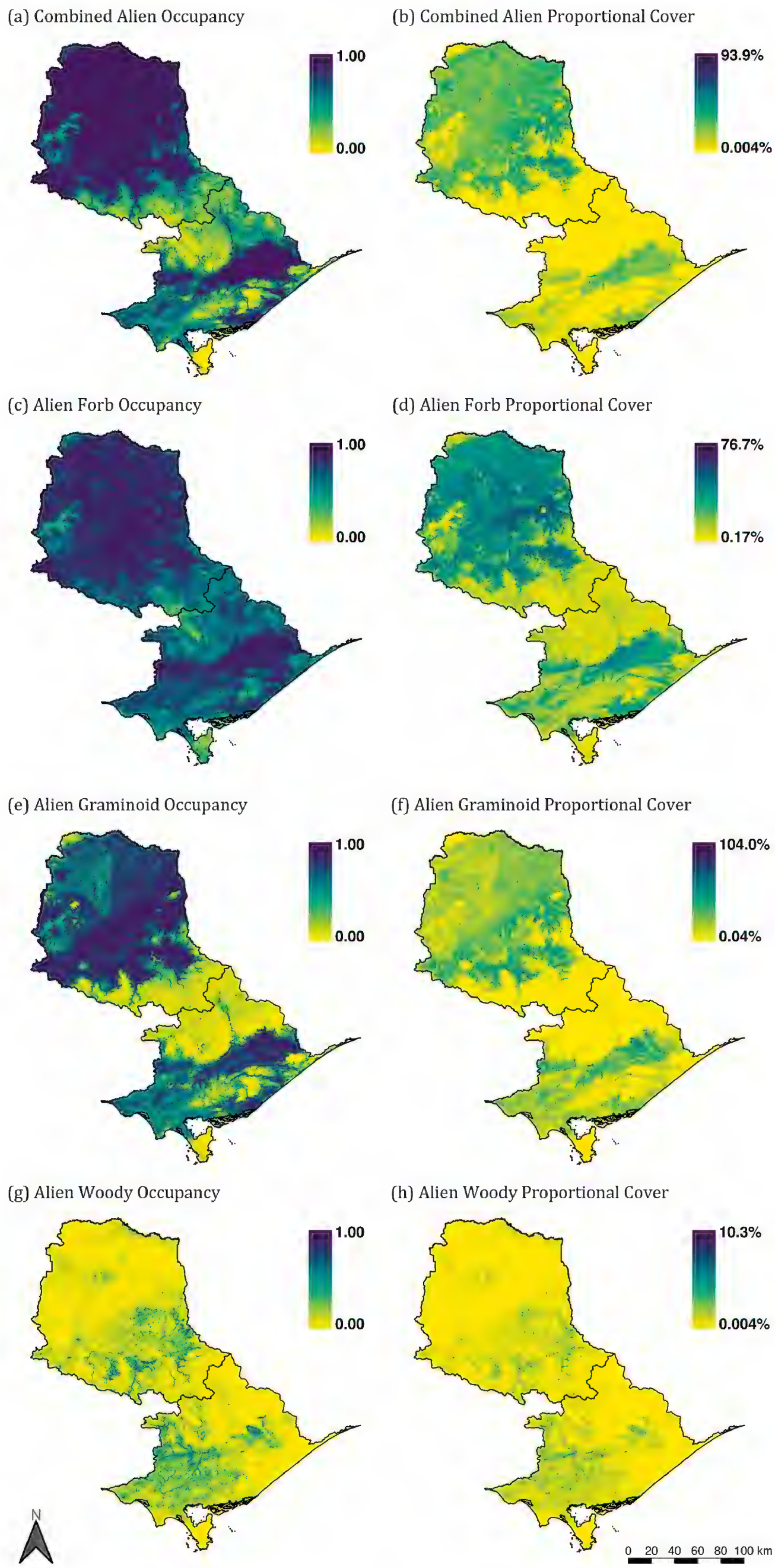

Figure 6. Maps showing predicted probability of occupancy (left panels) and proportional cover, dependent on the probability of occupancy (right panels), for: **a, b.** Combined alien taxa; **c, d.** Alien forbs; **e, f.** Alien graminoids and **g, h.** Alien woody vegetation in 2020.

the boosted regression tree (BRT) model results confirm that plant invasion is multifaceted, driven by interactions between propagule pressure, biotic and abiotic conditions and influenced by human activity (Fig. 2; Catford et al. (2009); Pyšek et al. (2020a); Hulme et al. (2023)). The most vulnerable areas to invasion in the 42,000 km^2 study region were in lower elevation regions close to human activity, especially for forbs and graminoids, which reached higher predicted levels of occupancy and cover abundance than woody alien vegetation, as has been found elsewhere (Mologni et al. 2022). Identifying both similarities and differences across plant growth forms can inform invasion science and management.

Factors associated with invasion of alien graminoids, forbs and woody plants

Variables indicating abiotic conditions (e.g. January mean maximum temperature, mean precipitation, geology, land-cover) had the strongest link with alien plant occupancy and cover abundance. This is consistent with hypotheses proposing that resource availability and climatic conditions are the major limiting factors of invasion (Davis et al. 2000; D'Antonio et al. 2017). However, it may have also reflected the spatial grain of our study, which was based on 30 m × 30 m quadrats. This scale may limit detection of biotic interactions, which typically manifest at finer resolutions, at least for herbaceous plants (Brian and Catford 2023; Pérez-Navarro et al. 2023). Occupancy and abundance of all growth forms were positively associated with summer maximum temperature, presumably because warmer conditions were more hospitable for plant growth regardless of invader growth form.

While temperature had a consistent relationship across response variables, relationships with quadrat vegetation cover varied, with alien occupancy generally increasing with vegetation cover and invader abundance declining. The positive relationship between alien herb occupancy and vegetation cover is consistent with ideas related to habitat filtering (Catford et al. 2009; Enders et al. 2020). Alien colonisation was likely elevated in high vegetation cover areas because the growing conditions were suitable for most plant species, thereby increasing the probability of alien plants being present (Catford et al. 2011). Conversely, proportional cover likely remained low in high-cover areas because of high competition from resident plants (Nunez-Mir et al. 2017). Unlike forbs and graminoids, alien woody occupancy and abundance both declined with increasing woody vegetation cover (Fig. 4). This may reflect biotic resistance from resident biota, but also likely reflects that denser woody vegetation is more intact, with likely lower levels of human-mediated disturbance and introduction of alien plant propagules. The relationships with vegetation cover highlight how invasion drivers can vary between growth forms and invasion stages (Catford et al. 2022).

Spatial patterns of invasion

Alien plant invasion was predicted to be highest in areas with intensive land use, where urban and agriculture are the dominant land-cover and areas immediately adjacent to roads where habitat is fragmented and propagule pressure and resource availability are high (Fig. 6). These patterns are consistent with those elsewhere and point to the role of human activities and human-mediated dispersal in facilitating invasion (González-Moreno et al. 2014; Rauschert et al. 2017; Szymura et al. 2018).

Despite similar responses of alien woody and herbaceous vegetation to human activities, there was variation in the levels and spatial distributions of the three growth forms examined (Fig. 6). Forbs could be found almost everywhere in the study region, though their cover was lower in the high elevation areas. Compared with alien forbs and woody vegetation, graminoid invasion was largely confined to lower elevation areas dominated by human activities and was much more limited in areas dominated by native vegetation, like in national parks and reserves and in the Great Dividing Range (Figs 1, 6). Giorgis et al. (2016) also found lower graminoid invasion in native woodlands. Woody invasion was much more limited than herbaceous invasion, which may reflect a range of factors including lower colonisation and propagule pressure, lower habitat suitability and shorter effective residence times (i.e. especially when considering species generation times).

There are some unusual spatial patterns of alien graminoid invasion in the north-west of Goulburn Broken catchment (Fig. 6e, f). This anomaly is likely due to the lower availability of field observation data across this region due to the intensive land-use practices associated with the provision of irrigation services. This has a concomitant effect of restricting access to land to undertake surveys and dampening observer interest. As such, the model is informed by data from the few larger public land blocks interacting with climate splines, resulting in an anomalous pattern of alien graminoid invasion.

The presence of weak, but statistically significant spatial autocorrelation in our occupancy models (see Suppl. material 1: appendix S1) underscores the importance of considering spatial processes in ecological modelling, even when using robust machine-learning methods like BRT. However, the low Moran's I values suggest these effects are modest and unlikely to compromise the overall model validity (Bini et al. 2006; Dormann et al. 2007). In contrast, the lack of significant autocorrelation in cover models supports the spatial adequacy of predictor variables in explaining variation in alien plant cover (see Suppl. material 1: appendix S1).

Management implications

Our study illustrates that invasion is driven by a suite of factors, many of them shared across different growth forms, highlighting multiple vulnerabilities and levers for management. Focusing on proportional abundance of alien taxa, our results suggest that further native vegetation loss will facilitate alien plant dominance in the study region. Deforestation, wildfire and other land-use changes that disturb native vegetation all pose a risk for further invasion. The study region – and south-eastern Australia more broadly – is prone to wildfire, as the devastating bushfires of 2019–2020 demonstrated, a risk that is set to rise as climate change strengthens (Turbelin and Catford 2021). Our results highlight the importance of maintaining or restoring native vegetation to limit alien plant dominance, especially for woody alien species that may otherwise struggle to colonise. By extension, our findings also confirm the value of actively managing alien plant populations, while native vegetation recovers from disturbances like fire (Lindenmayer et al. 2015).

As well as reducing native vegetation and associated biotic resistance, urban and agricultural expansion will increase habitat fragmentation and propagule pressure, likely increasing invasion in areas currently experiencing lower invasion levels (Boscutti et al. 2022). Based on our study, alien graminoids should benefit the most from this sort of land-cover change (Fig. 6e, f). In conjunction with increasing

wildfire risk, climate change is expected to facilitate further invasion in the study region by raising temperatures (Fig. 3, Catford and Jones (2019)). Counteracting these changes (among others; Nolan et al. (2021)) through local and regional management measures, like strategic land-use planning or vegetation restoration, will be important for limiting further invasion (O'Reilly-Nugent et al. 2024).

Identifying common drivers of invasion, and regions highly susceptible to invasion, can help prioritise areas for management actions. While useful to examine trends of all alien plants combined, grouping species by growth form enables more targeted science and management. For example, the efficacy of certain weed control methods, including herbicide, can vary across growth forms. Single-species models will remain a key tool in understanding and managing invasive plants, but more general models based on plant growth form offer an efficient and informative approach for assessing plant invasion across variable landscapes.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

JC, DG & MW conceptualised the study; MW provided the data; DG undertook the modelling; DG wrote the first draft of the manuscript; all authors contributed to later versions of the manuscript; JC acquired funding and supervised the project.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Similar drivers but distinct patterns of woody and herbaceous alien plant invasion

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Data type: docx

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